

Subnasal Morphological Variation in Fossil Hominids: A Reassessment Based on New Observations and Recent Developmental Findings

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ABSTRACT Quantitative and qualitative assessments of subnasal morphology in fossil hominids yield distinct patterns which have been used both to sort robust from nonrobust australopithecine taxa and to distinguish individual species. Recently, new developmental models have been applied to hominoid subnasal morphological variation. These studies require that certain features of the fossil hominid subnasal region, in particular the topography of the nasal cavity entrance and details of vomeral morphology, be reevaluated. This study does so for the robust and nonrobust australopithecines, early *Homo* (*H. habilis*/*H. rudolfensis*), and African *H. erectus*. Results reaffirm an overall similarity of the nonrobust *Australopithecus* subnasal morphological pattern with that of the chimpanzee. They further indicate that a vomeral insertion above the nasal surface of the premaxilla should be added to the list of traits characteristic of the robust australopithecine subnasal morphological pattern. Finally, reassessment of subnasal morphology in the early *Homo* and *H. erectus* samples from Africa suggest that these two taxa share a similar subnasal morphological pattern. This pattern consists of a smooth nasal cavity entrance, a horizontal nasal sill whose anterior edge is demarcated by a strong nasal crest, and a well-developed horizontal spine at the posterior edge of the nasal sill. Although none of the African fossil *Homo* specimens preserve a vomer, indirect evidence suggests that it would have inserted above the nasal sill. *Am J Phys Anthropol* 112:275–283, 2000. © 2000 Wiley-Liss, Inc.

Over 30 years ago, Robinson (1953, 1954) described morphologically diagnostic subnasal patterns that differed in three hominid species (i.e., *Paranthropus robustus*, *Australopithecus africanus*, and “*Telanthropus capensis*” = *Homo erectus*). More recently, McCollum et al. (1993) evaluated Robinson’s original findings in light of an expanded fossil record. The latter study, which considered a large number of both qualitative and quantitative features of the subnasal region, confirmed the existence of distinct subnasal morphological patterns which sort robust from nonrobust australo-

pithecine taxa, and which distinguish individual species as well. In contrast, a consistent morphological pattern could not be identified for either the early *Homo* (i.e., *H. habilis*/*H. rudolfensis*) or African *H. erectus* samples. However, the fossil *Homo* samples examined by McCollum et al. (1993) were

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quite small, and many of the included specimens were poorly preserved.

Since the publication of McCollum et al. (1993), studies of extant hominoid subnasal variation have begun to shed light on the underlying developmental basis of the distinct morphological patterns that characterize hominoid taxa (McCollum, 1997; McCollum and Ward, 1997). As a result of this added perspective, certain features of the fossil hominid subnasal region require reevaluation. Also of consequence is the inclusion within the African fossil *Homo* sample of new specimens from Kenya (i.e., KNM-WT 15000; Walker and Leakey, 1993) and Ethiopia (i.e., AL 666-1; Kimbel et al., 1997). These specimens, in which the morphology of the subnasal region is well-preserved, allow for a more detailed assessment of fossil *Homo* subnasal morphology. The purpose of this paper is to reassess and clarify fossil hominid subnasal morphological variation in light of these recent events.

MATERIALS AND METHODS

With a few exceptions, all morphological observations discussed here are of the original fossil material. The South African hominid fossils were examined at the Transvaal Museum, Pretoria and the Department of Anatomy, University of the Witwatersrand. Specimens of *A. boisei* and *Homo*, as well as the KNM-WT 17000 cranium, were examined at the National Museums of Kenya, Nairobi. Observations of *A. afarensis* specimens AL 199-1, 200-1, and 333-1, the *A. boisei* OMO-323 maxilla and OH 5 cranium, and the OH 24 and OH 62 early *Homo* specimens are of casts of the original specimens housed at Kent State University. The AL 666-1 early *Homo* maxilla from Hadar was not examined as part of this study.

For the australopithecine specimens, features of interest include the topography of the nasal entrance and morphological relations of the anterior tip of the vomer. In addition to these two features, the *Homo* sample was further assessed with respect to the presence/absence of nasal crests. The specific details of these features are provided below.

RESULTS

Topography of the nasal cavity entrance

The "topography" of the nasal cavity entrance refers to the extent of vertical relief present at the transition between the premaxilla (or *os incisivum* of modern humans) and the palatine process of the maxilla at the entrance to the nasal cavity. This feature is typically scored as "stepped," implying some vertical relief (either gradual or abrupt), or "smooth," implying no detectable change of relief between subnasal elements. In McCollum et al. (1993), nasal floor topography was scored lateral to the incisive fossa.

A problem with conventional scoring of nasal floor topography is the identification of only two topographies (i.e., "stepped" vs. "smooth"). In reality, extant hominoids display a variety of subnasal topographies, most of which are subtle variations of what is best described as "continuous" (McCollum and Ward, 1997). A continuous transition between subnasal elements lateral to the incisive fossa makes sense in terms of nasal cavity development. During ontogeny, the nasal skeleton expands through resorption and drift of its lateral walls and floor, as mediated by the expanding mucosae lining these surfaces (Enlow and Hans, 1996). Unless superceded by other factors (e.g., incisor roots encroaching upon the anterior nasal cavity floor, or vertical inclination of the incisors and premaxilla), growth of the nasal mucosae will result in the three bones of the nasal cavity floor (i.e., palatine, maxilla, and premaxilla/*os incisivum*) being modeled as a single continuous element. This is clearly evident in the smooth nasal floors of extant orangutans and modern humans. A continuous, subtle transition between subnasal elements lateral to the incisive fossa is also characteristic of chimpanzees. In fact, this transition is so subtle that in previous studies, approximately 30% of adult chimpanzees were scored as possessing smooth (= no relief) nasal cavity floors lateral to the incisive fossa (McCollum et al., 1993; McCollum and Ward, 1997).

Among large-bodied hominoids, only *Gorilla* consistently displays a noncontinuous,

stepped nasal floor topography in which there is an extensive change in elevation from the premaxilla onto the palatine process along the full extent of the nasal cavity entrance (McCollum and Ward, 1997). The consistent association of this topography with additional subnasal features not found in other extant hominoid taxa (e.g., enlarged prevomer, posteriorly-placed anterior nasal tubercle) suggests that the *Gorilla* morphology is a derived condition within extant hominoids (McCollum and Ward, 1997). Based on these more recent findings, it is inappropriate to continue to characterize chimpanzees and gorillas as possessing similar subnasal topographies. Rather, the variation in subnasal topography present in extant hominoids suggests that three subnasal topographies should be identified: 1) "continuous-smooth," implying a continuous transition between subnasal elements with no detectable change in relief between the premaxilla and palatine process of the maxilla, 2) "continuous-discrete," referring to a continuous transition between subnasal elements with some vertical relief between the premaxilla and maxillary palatine process, and 3) "interrupted," referring to the presence of an extensive change in elevation between the premaxilla and palatine process lateral to the incisive fossa.

The topography of the nasal cavity entrance is one of several subnasal features identified by McCollum et al. (1993) that can be used to sort nonrobust and robust australopithecines. Specifically, it was found that both *A. afarensis* and *A. africanus* display a stepped nasal cavity entrance, while the nasal cavity entrance in all robust australopithecine specimens (including the KNM-WT 17000 cranium) is smooth. The change in elevation that occurs between the premaxilla and the palatine process in non-robust australopithecines is, however, quite subtle and is most similar to that characteristic of chimpanzees. As such, it is more appropriate to characterize the nasal floor topographies of these specimens as continuous-discrete, rather than stepped.

With respect to the fossil *Homo* sample, McCollum et al. (1993) reported considerable variation in the topography of the nasal cavity entrance in both the early *Homo* and

African *H. erectus* samples (Table 1). In that study, a stepped nasal cavity entrance was reported for KNM-ER 1813, OH 24, KNM-ER 3733, SK 847, and KNM-ER 1470. Smooth nasal floor topographies were reported for KNM-ER 1805, Stw 53, and OH 62. Despite these previous characterizations, observations of the original specimens clearly reveal that the transition between subnasal elements is not preserved lateral to the incisive fossa in KNM-ER 1813, SK 847, or Stw 53. Consequently, this feature cannot be scored in any of these specimens. Of the remaining fossil *Homo* specimens, the subnasal region of KNM-ER 1470 is so heavily damaged and extensively eroded that evaluation of its subnasal morphology is not advisable. Similar conclusions were reached with respect to KNM-ER 1805, in which distortion of this specimen precludes meaningful analysis of its subnasal morphology. With respect to the KNM-ER 3733 cranium, the original specimen displays extensive damage in the subnasal region not noted by McCollum et al. (1993). Accordingly, it cannot be determined whether the deep drop into the nasal cavity that is present in this specimen represents actual morphology, or is instead simply an artifact of preservation.

Of the early *Homo* and African *H. erectus* specimens currently available, only KNM-WT 15000, OH 62, and AL 666-1 preserve the transition between the premaxilla and palatine process of the maxilla lateral to the incisive fossa. As originally reported by Rightmire (1998), the nasal cavity entrance of KNM-WT 15000 is smooth lateral to the incisive fossa. A similar morphology is observed in OH 62. With respect to the AL 666-1 maxilla, Kimbel et al. (1997) report that the nasal cavity topography of this specimen shows strong similarities to that of KNM-WT 15000, KNM-ER 3733, SK 847, and Sangiran 4. From the superior view of this specimen (Fig. 4A of Kimbel et al., 1997), it appears as though the nasal cavity entrance of this specimen is smooth lateral to the incisive fossa.

Vomer insertion

In his revision of South African australopithecine taxonomy, Robinson (1954) noted

TABLE 1. Qualitative features of the early hominid subnasal region

Taxon	Specimen	Nasal entrance ¹	Nasal entrance ²	Vomer height ¹	Vomer insertion ²
<i>Pongo pygmaeus</i>		Smooth	Continuous-smooth	Variable	Variable/below
<i>Gorilla gorilla</i>		Stepped	Interrupted	Variable	Variable/below
<i>Pan troglodytes</i>		Stepped	Continuous-discrete	Variable	Variable/below
<i>Homo sapiens</i>		Smooth	Continuous-smooth	High	High/above
<i>A. afarensis</i>	AL 199-1	Stepped	Continuous-discrete	N/A ³	N/A
	AL 200-1	Stepped	Continuous-discrete	High	High/below
	AL 333-1	Stepped	Continuous-discrete	High	High/below
<i>A. africanus</i>	MLD 9	Stepped	Continuous-discrete	Intermediate	Intermediate
	MLD 45	Stepped	Continuous-discrete	N/A	N/A
	TM 1512	Stepped	Continuous-discrete	N/A	N/A
	Sts 5	Stepped	Continuous-discrete	Low	Intermediate
	Sts 17	Stepped	Continuous-discrete	Low	Intermediate
	Sts 52a	Stepped	N/A	Low	Intermediate
	Sts 71	Stepped	Continuous-discrete	Low	N/A
	Stw 73	Stepped	Continuous-discrete	Low	Intermediate
<i>A. robustus</i>	TM 1517	Smooth	Continuous-smooth	N/A	N/A
	SK 12	Smooth	Continuous-smooth	Low	High/above
	SK 13/14	Smooth	N/A	N/A	N/A
	SK 46	Smooth	Continuous-smooth	Intermediate	High/above
	SK 47 ⁴		Continuous-smooth		High/above
	SK 48	Smooth	Continuous-smooth	Intermediate	N/A
	SK 52	Smooth	Continuous-smooth	Intermediate	High/above
	SK 65	N/A	Continuous-smooth	N/A	N/A
	SK 83	Smooth	Continuous-smooth	N/A	N/A
	SKW 8	Smooth	Continuous-smooth	N/A	N/A
	SKW 11	Smooth	N/A	Low	High/above
	SKX 265	Smooth	Continuous-smooth	Low	N/A
<i>A. boisei</i>	KNM-CH1	Smooth	Continuous-smooth	N/A	High/above
	KNM-ER 405	Smooth	Continuous-smooth	N/A	N/A
	KNM-ER 406	Smooth	Continuous-smooth	High	High/above
	OH 5	Smooth	Continuous-smooth	N/A	N/A
	OMO 323	Smooth	Continuous-smooth	N/A	N/A
	KNM-WT 17000	Smooth	Continuous-smooth	High	High/above
<i>Early Homo</i>	KNM-ER 1470	Stepped?	N/A	N/A	N/A
	KNM-ER 1805	Smooth	N/A	N/A	N/A
	KNM-ER 1813	Stepped	N/A	Low	N/A
	OH 24	Stepped	N/A	N/A	N/A
	OH 62	Smooth	Continuous-smooth	N/A	N/A
	Stw 53	Smooth	N/A	N/A	N/A
<i>H. erectus</i>	KNM-ER 3733	Stepped	N/A	N/A	N/A
	SK 847	Stepped	N/A	High	N/A
	KNM-WT 15000 ³		Continuous-smooth		N/A

¹ As originally scored by McCollum et al. (1993).² As reassessed in this study.³ Not applicable.⁴ Specimen not included in original study.

that the height at which the anterior tip of the vomer contacts the anterior nasal spine or tubercle clearly distinguishes robust from nonrobust australopithecine taxa. Following Robinson (1954), McCollum et al. (1993) assessed the height of the vomeral insertion for all specimens which preserve this morphology. In that study, the vertical distance

separating the point representing the maximum height of the anterior tip of the vomer from that representing the most anterior attachment of the cartilaginous nasal septum was scored as being either "low" (vomer inserts within incisive fossa/canal and does not contact the premaxilla), "intermediate" (vomer inserts within incisive fossa/canal

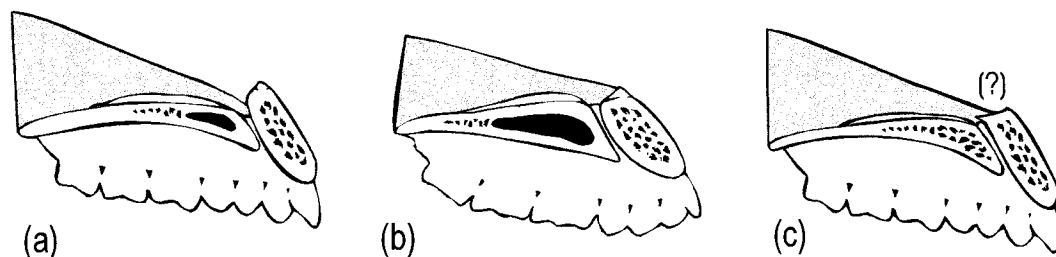


Fig. 1. Sagittal sections of the (a) *A. africanus*, (b) *A. robustus*, and (c) fossil *Homo* subnasal regions as taken lateral to the nasal septum and looking medially. The anterior tip of the vomer (shaded) inserts below the nasal sill in *A. africanus* and above the nasal sill in the robust australopithecine. Note the relative flatness and posteriorly projecting spine of the nasal sill in fossil *Homo*.

and contacts the premaxilla), or “high” (vomer inserts at the elevation of the cartilaginous septum attachment or on the superior surface of the nasal sill). Details of the vomeral insertion were, in the majority of cases, identified from casts of the original specimens prepared specifically for that study. Results obtained by McCollum et al. (1993) revealed fairly consistent variation in the height of the vomeral insertion within taxa and were therefore considered consistent with the earlier findings (Table 1). Although not emphasized, Robinson (1954) nevertheless recognized that the vomeral insertions of robust and nonrobust australopithecine taxa also vary with respect to the relationship they maintain with the *nasal sill*, i.e., the nasal surface of the premaxilla. According to his own illustrations (Fig. 2 of Robinson, 1954), the anterior tip of the vomer in *A. africanus* inserts behind and below the nasal sill. In comparison, the vomer in *A. robustus* extends onto the nasal sill to insert at the back of the anterior nasal tubercle (compare Fig. 1a,b). This particular aspect of the vomeral insertion was not examined in the previous study.

Table 1 lists the qualitative features of the early hominid subnasal region as originally reported by McCollum et al. (1993) and as reassessed here. As in the previous study, vomeral height was scored here as low, intermediate, or high. In addition, for those specimens in which vomeral height was found to be high, the vomeral insertion was further characterized as occurring either “above” or “below” the nasal sill, with “below” referring to vomers that terminate either behind or below the premaxilla. As

Table 1 demonstrates, the characterization of the vomeral morphology of a number of specimens has changed following evaluation of the original specimens. For example, in the original study, the majority of *A. africanus* specimens (Sts 5, Sts 17, Sts 71, and Stw 73) were scored as possessing low vomeral heights. However, in this study, contact between the vomer and the posterior pole of the premaxilla indicative of an intermediate vomeral height was observed in Sts 5, Sts 17, and Sts 52A (previously scored as unknown). In addition, although a number of *A. robustus* specimens were scored as possessing low or intermediate vomeral heights, some of these specimens (SK 48, SKX 265) preserve insufficient detail of their vomeral morphology to accurately characterize this feature. In other *A. robustus* specimens, including SK 12, SK 46, SK 47, and SK 52, the anterior tip of the vomer is preserved at its insertion above the nasal sill. In the *A. boisei* sample, a vomeral insertion above the nasal sill characterizes KNM-ER 406 and KNM-CH 1. A similar vomeral morphology was observed in the KNM-WT 17000 cranium. Details of the vomeral insertion could not be determined in any fossil *Homo* specimen.

Nasal crests

As summarized by Gower (1923), the following three ridges enter into the formation of the lower border of the nasal aperture of humans: 1) a lateral crest arising from the lateral margin of the nasal aperture, 2) a spinal crest originating from the nasal “spine,” and 3) a turbinal crest originating from near the anterior end of the inferior

turbinate. The many different possibilities of development and fusion of these ridges contribute to the overall variability of the nasal cavity floor and render their accurate identification in highly fragmentary specimens difficult, if not impossible.

In his description of the SK 80 "Telanthropus" maxilla (now part of SK 847; Clarke, 1977), Robinson (1953) noted that the nasal sill of this specimen takes the form of a horizontal platform, the anterior edge of which is formed by a small ridge emanating laterally from the anterior nasal spine/tubercle and whose well-defined posterior edge is transformed into a spine for receipt of the vomer (Fig. 1c). Unfortunately, the complete absence in this specimen of any remnant of the lateral nasal walls prevents determination of the actual source of the crests that form the anterior and posterior edges of the bony platform. Based on the studies by Gower (1923) on nasal crests in modern humans, it is most likely that the posterior edge of the SK 847 nasal platform represents fused spinal and turbinal crests, while the anterior edge represents a lateral crest that has extended to the midline. It is also possible, but less likely, that the posterior and anterior edges are formed by turbinal and spinal crests, respectively.

Due to either the poor preservation of many of the representative specimens, or the concealment of the posterior edge of the nasal sill by matrix in available casts, McCollum et al. (1993) were unable to identify a nasal platform similar in form to that of SK 847 in any of the fossil *Homo* specimens included in their sample. However, observation of the original specimens now reveals that a horizontal nasal sill virtually identical to that of SK 847 is present in KNM-ER 1813, Stw 53 (Hughes and Tobias, 1977), and KNM-WT 15000. In addition, a distinct crest forming the anterior border of the nasal cavity floor is preserved on the right side of the lower nasal margin in KNM-ER 3733. Kimbel et al. (1997) report that an anteriorly demarcated "elevated intranasal platform" similar to that of KNM-ER 1813 is characteristic of AL 666-1 as well. The morphology of the posterior nasal sill is obscured in all available casts of the OH 24 specimen.

DISCUSSION

Australopithecine subnasal morphology

According to McCollum et al. (1993), *A. afarensis* and *A. africanus* share a subnasal morphological pattern that consists of a stepped nasal cavity floor, a broad incisive fossa, and an anterior attachment of the nasal septum that occurs slightly behind the plane formed by the lateral margins of the nasal aperture. This morphological pattern was considered primitive because of its strong resemblance to that of chimpanzees. Subnasal features which distinguish *A. afarensis* from *A. africanus* include the contours of the lateral margins of the nasal aperture (sharp vs. rounded), the height of the vomeral insertion (high vs. low), and the distribution of crests along the nasal cavity floor (see McCollum et al., 1993). Reassessment of subnasal features in the original specimens indicates that the nasal floor topographies of these specimens are better described as continuous-discrete as opposed to stepped. In addition, rather than displaying a consistently low vomeral height, as was originally reported, it is now apparent that the anterior tip of the vomer in most *A. africanus* specimens contacts the posterior pole of the premaxilla as it descends into the incisive canal. The vomer in this taxon is therefore intermediate in height relative to that of the anterior nasal tubercle.

White et al. (1981) concluded that the majority of features that distinguish the lower face of *A. afarensis* from that of *A. africanus* reflect variation in the size and morphology of the maxillary incisors. For example, because the *A. afarensis* incisors are large and their roots are robust and curved, the nasoalveolar clivus in this species is also wide and curved. In addition, the sharp lateral margins of the nasal aperture observed in *A. afarensis* were viewed as being the result of their position medial to the lateral incisors. In comparison, the relatively narrow incisors of *A. africanus* result in a relatively narrow clivus and a nasal aperture whose lateral margins are rounded because they are buttressed by the canine juga. In *A. africanus*, both the roots of the maxillary incisors and the nasoalveolar clivus are comparatively straight. Whether the varia-

tion in vomeral height observed between the two nonrobust taxa is related to variation in incisor morphology is presently unclear.

With respect to the robust forms, McCollum et al. (1993) concluded that *A. robustus* and *A. boisei* share a common subnasal morphological pattern that consists of a thickened hard palate, a substantial amount of overlap between subnasal elements, a continuous-smooth nasal cavity entrance lateral to the incisive fossa, and rounded lateral margins of the nasal aperture. Although it was originally concluded that the height of the vomeral insertion differed between the robust taxa, results of the present study indicate that the vomer inserts above the premaxilla in both *A. robustus* and *A. boisei*. Consequently, this trait also distinguishes robust and nonrobust australopithecine taxa. Although remarkably similar overall, the subnasal morphologies of *A. robustus* and *A. boisei* are not identical. As was reported previously (McCollum et al., 1993), the anterior-posterior length of the nasal sill is much greater in *A. boisei* than it is in *A. robustus*. In addition, the anterior nasal tubercle of *A. robustus* is typically (but not universally, e.g., SKX 265) recessed within the nasal cavity. In all *A. boisei* specimens which preserve this morphology, the anterior nasal tubercle occurs in the same plane as the lateral margins of the nasal aperture.

Of the derived subnasal features shared by robust australopithecine taxa, a vomeral insertion above the nasal sill may be the most significant. From the perspective of nasal floor remodeling, the extension of the vomer across the sutural interface separating the anterior nasal sill from the more posterior aspects of the nasal cavity floor may have had the effect of constraining the anterior and posterior nasal floor surfaces to maintain the same approximate horizontal level throughout the growth process (McCollum, 1997, 1999). If so, then the continuous-smooth nasal floor of the robust taxa is simply a developmental correlate of a vomeral insertion above the nasal sill. Significantly, a similar correlation of a continuous-smooth nasal floor topography with a vomeral insertion above the nasal sill is found in modern humans (McCollum et al., 1993; McCollum

and Ward, 1997). In addition, through its influence on the pattern of nasal floor remodeling that would have accompanied extensive vertical growth of the mandibular ramus (Bromage, 1989), it is also likely that the derived vomeral insertion of the robust australopithecines would have contributed to the extreme palatal thickening characteristic of these taxa (McCollum, 1997, 1999). Based on the morphology of modern humans, who, in addition to their vomeral morphology, also share with robust australopithecines a small anterior dentition, it is reasonable to suggest that a vomeral insertion above the nasal sill is related to the possession of small anterior teeth. Further evaluation of this particular aspect of robust australopithecine subnasal morphology is currently underway.

Homo

It was originally reported by McCollum et al. (1993) that considerable variation in the morphology of the early *Homo* subnasal region prevents the identification of a subnasal morphological pattern specific to this group. However, the new observations of the original specimens reported here indicate that much of this "variation," especially that pertaining to nasal entrance topography, is simply a product of exceedingly poor preservation of the early *Homo* sample (see Results). Although the number of well-preserved fossil *Homo* specimens is still quite small ($n = 3$), all display a smooth nasal cavity entrance lateral to the incisive fossa, a nasal sill in the form of a horizontal platform demarcated anteriorly by nasal crests, and a horizontal spine at the posterior edge of the nasal sill for receipt of the vomer. Despite their poor quality, the remainder of the fossil *Homo* specimens display certain consistencies with the more complete specimens. For example, KNM-ER 1813, Stw 53, and SK 847 each possess remnants of a horizontal nasal sill. In addition, in Stw 53 and SK 847, a horizontal spine projects posteriorly from the nasal sill. It is unfortunate that none of the fossil *Homo* specimens preserve details of their vomeral insertion. However, the presence of smooth nasal floor topographies in these specimens suggests

that the vomer most likely inserted above the nasal sill.

In his description of the SK 80 (SK 847) maxilla, Robinson (1954) noted that the preserved subnasal morphology of this highly fragmentary specimen is very reminiscent of the modern human condition. Additional information provided by relatively more complete specimens (i.e., AL 666-1, KNM-WT 15000) confirms that an essentially modern human nasal cavity floor morphology, complete with a smooth nasal cavity entrance, horizontal nasal sill, and posterior spine, characterizes both the early *Homo* and African *H. erectus* samples. Furthermore, as has been demonstrated by Rightmire (1998), a similar subnasal morphological pattern is found in Asian *H. erectus*. Of the Asian specimens that display elements of this subnasal pattern (Gongwangling, Sangiran 4, and Sangiran 17), Sangiran 4 is especially informative as it preserves a vomeral insertion which, based on the description by Rightmire (1998), does indeed occur above the nasal sill.

Of the early *Homo* and *H. erectus* specimens currently known, only OH 24 (McCollum et al., 1993) and Sangiran 17 (Kimbel et al., 1997; Rightmire, 1998) display a projecting anterior nasal spine. The developmental basis of the anterior nasal spine of humans, the presence of which is variable in modern populations, is a matter of some debate (Mooney and Siegel, 1991; Simpson and McCollum, 1993; Braga, 1998). The general absence of an anterior nasal spine in the earliest members of the genus *Homo* could reflect either a primarily depositional nasoalveolar clivus (or at least one that fails to resorb), a comparatively greater anterior growth movement of the incisive region (affected by prolonged growth at the premaxillary/maxillary or incisive sutures), or both.

CONCLUSIONS

The purpose of this study was to reassess fossil hominid subnasal morphological variation in light of new data provided by developmental studies of subnasal form and recently recovered fossil specimens. The results reaffirm the primitive nature of the nonrobust *Australopithecus* subnasal morphological pattern and its similarity to that

of common chimpanzees. It has also been demonstrated that a vomeral insertion that occurs above the nasal sill should be added to the list of subnasal features that characterize robust australopithecine taxa. Finally, reassessment of subnasal morphology in the original fossil *Homo* sample from Africa reveals that these specimens share with Asian *H. erectus* a subnasal morphological pattern which consists of a smooth nasal cavity floor, a horizontal nasal sill demarcated by well-developed nasal crests, and a horizontal spine at the vomeral insertion. Although none of the fossil *Homo* specimens from Africa actually preserve a vomer, indirect evidence suggests that it inserted above the nasal sill, much as it does in modern humans.

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LITERATURE CITED

- Braga J. 1998. Chimpanzee variation facilitates the interpretation of the incisive suture closure in South African Plio-Pleistocene hominids. *Am J Phys Anthropol* 105:121-136.
- Bromage TG. 1989. Ontogeny of the early hominid face. *J Hum Evol* 23:235-251.
- Clarke RJ. 1977. The cranium of the Swartkrans hominid SK 847 and its relevance to human origins. Ph.D. Dissertation, University of the Witwatersrand.
- Enlow DH, Hans MG. 1996. Essentials of facial growth. Philadelphia: W.B. Saunders Co.
- Gower CD. 1923. A contribution to the morphology of the apertura piriformis. *Am J Phys Anthropol* 6:27-36.
- Hughes AR, Tobias PV. 1977. A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature* 265:310-312.
- Kimbel WH, Johanson DC, Rak Y. 1997. Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *Am J Phys Anthropol* 103:235-262.

- McCollum MA. 1997. Palatal thickening and facial form in *Paranthropus*: examination of alternative developmental models. *Am J Phys Anthropol* 103:375–392.
- McCollum MA. 1999. The robust australopithecine face: a morphogenetic perspective. *Science* 284:301–305.
- McCollum MA, Ward SC. 1997. Subnasalveolar anatomy and hominoid phylogeny: evidence from comparative ontogeny. *Am J Phys Anthropol* 102:377–405.
- McCollum MA, Grine FE, Ward SC, Kimbel WH. 1993. Subnasal morphological variation in extant hominoids and fossil hominids. *J Hum Evol* 24:87–111.
- Mooney MP, Siegel MI. 1991. Premaxillary-maxillary suture fusion and anterior nasal tubercle morphology in the chimpanzee. *Am J Phys Anthropol* 85:451–456.
- Rightmire GP. 1998. Evidence from facial morphology for similarity of Asian and African representatives of *Homo erectus*. *Am J Phys Anthropol* 106:61–86.
- Robinson JT. 1953. *Telanthropus* and its phylogenetic significance. *Am J Phys Anthropol* 11:445–502.
- Robinson JT. 1954. The genera and species of the Australopithecinae. *Am J Phys Anthropol* 12:181–200.
- Simpson SW, McCollum MA. 1993. Premaxilla in African apes: comment on Mooney and Siegel (1991). *Am J Phys Anthropol* 90:247–252.
- Walker AC, Leakey RE. 1993. The skull. In: Walker AC, Leakey RE, editors. *The Nariokotome Homo erectus* skeleton. Cambridge, MA: Harvard University Press. p 63–94.
- White TD, Johanson DC, Kimbel WH. 1981. *Australopithecus africanus*: its phyletic position reconsidered. *S Afr J Sci* 77:445–470.